A REAPPRAISAL OF *PROPHAETHON SHRUBSOLEI* ANDREWS (AVES)

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CONTENTS

ABSTRACT

Prophaethon shrubsolei Andrews of the Lower Eocene, known from an imperfect skeleton, has been previously assigned to the Phaethontidae within the Pelecaniformes. After further preparation the specimen is redescribed. In comparison with Recent species of Pelecaniformes, Charadriiformes and Procellariiformes it was found to share some characters with all three, and could not with any certainty be assigned to any one of them. It is proposed, therefore, that *Prophaethon* should be considered as a representative of a new monotypic order, Prophaethontiformes, and it is suggested that it represents an early link between these Recent orders. This hypothesis is discussed and a diagnosis of the new order is given.

I. INTRODUCTION

In 1899 C. W. Andrews described a fossil bird which W. H. Shrubsole had collected from the London Clay of the Isle of Sheppey, Kent, and had presented to the British Museum (Natural History). When found, the specimen consisted of a clay nodule in which one side of the skull and limb fragments were exposed. It was partially prepared at the Museum and when described and figured it showed the entire dorsal, posterior and right lateral views of the skull with the lower mandible in place. The orbit was also partly cleared of matrix back to the quadrate and down to the quadratojugal bar. The left side of the pelvis, which was somewhat obscured by the overlying skull, was also prepared, and a femur and the anterior portion of a broken tibiotarsus were laterally exposed.

From the general appearance of the skull Andrews concluded that it belonged to a pelecaniform bird. In the subsequent discussion of its affinities only pelecaniform families were referred to, and one may conclude that once he had decided on its possible ordinal status he did not compare it with material other than that within this taxon.

He compared the specimen systematically with examples of the various pelecaniform families and concluded that it most nearly resembled the genus *Phaethon* which constitutes the family Phaethontidae. In spite of some differences he thought that it was ancestral to *Phaethon* and named it *Prophaethon shrubsolei*, regarding the general similarities of the skull and deep fronto-nasal hinge with a prominent frontal ridge as evidence of affinity.

He noted that the nostrils of *Prophaethon*, unlike the holorhinal ones of *Phaethon*, approximated to the schizorhinal condition, but quoted Pycraft (1898) to the effect that on the skull of the young of *Phaethon* the nostrils show a nearly schizorhinal condition. He also noted that the pelvis was narrow and more closely resembled that of *Sula* and *Phalacrocorax*. He regarded the nostril condition as ancestral and concluded that the narrow pelvis indicated that, unlike the Recent *Phaethon*, *Prophaethon* was probably a good swimmer and diver, and that the extent to which *Phaethon* had diverged from this condition was a result of post-Eocene evolution.

During work towards a comprehensive review of the British Lower Eocene birds, still in progress, we decided that the specimen was suitable for further preparation by modern techniques. This was undertaken by Mr F. M. P. Howie of the Palaeontological Laboratory of the Museum. X-ray photographs were used to trace the position and extent of the bones present, and the specimen was then carefully prepared. As a result of this work most of the elements have now been separated and cleaned. The skull can be examined in all aspects including the palate (the lack of access to which Andrews regretted). The lower jaw is now separate and complete. A previously unsuspected portion of sternum has been revealed, and the hidden part of the proximal end of the tibiotarsus is now free. The pelvis has been extensively cleared, but still has attached to it the proximal half of the femur, and also portions of the ribs. An almost complete coracoid and the blade of a scapula are also present, and there are fragments of vertebrae and broken portions of limb-bones partly embedded in more resistant matrix.

In the following sections the various parts have been described. The terminology follows that of Jollie (1957) for the skull, and that of Howard (1929) for the post-cranial skeleton. From the characters now available the species does not appear to be closely allied to *Phaethon* and some characters are apparently shared with non-pelecaniform taxa.

II. DESCRIPTION

a. *Skull morphology*

Cranial and orbital structures. Viewed dorsally (Fig. 1 ; Pl. 1, fig. A) and laterally (Fig. 2 ; Pl. 1, figs C & D) the skull as a whole shows a fairly even taper from its widest part in the temporal region to its narrow termination at the tip of the rostrum. The frontal rises a little from the dorsal edge of the parietals, with a slight inflation on either side in the area above the brain. From near the posterior edge of the orbits the frontal maintains a fairly even width anteriorly, with a shallow median hollow in the interorbital region, and then expands gradually at the anterior

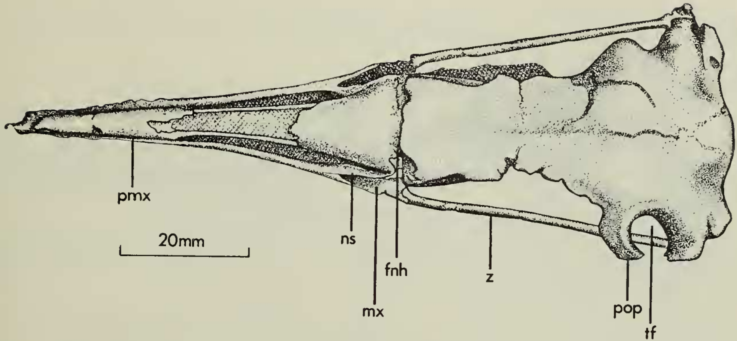

FIG. 1. Dorsal view of skull, × 1. Abbreviations : boc, basioccipital condyle ; bps, basiparasphenoid ; dps, gland depression, ? salt ; exn, external nares ; fm, foramen magnum ; fnh, fronto-nasal hinge ; ios, interorbital septum ; mx, maxilla ; ns, nasal strut ; pes, prefrontal attachment area ; pl, palatine ; pmx, premaxilla ; pop, postorbital process ; q, quadrate ; rps, rostroparasphenoid ; tf, temporal fossa ; z, zygoma.

end before terminating abruptly in a transverse, rounded and prominent brow ridge just above the fronto-nasal hinge. From the more complete left side of the frontal end of the specimen it would appear to be thick anteriorly, but above the orbits the frontal becomes very thin and its outer edge may have been irregular.

The posterior dorsal edge of the orbit curves outwards and terminates in a prominent, posteriorly curved postorbital process, which projects at a level only a little below the dorsal surface of the frontal. Posterior to this process is a deep temporal fossa. Viewed from above (Fig. 1 ; Pl. 1, fig. A), the fossa is rounded and partly enclosed by the postorbital process. In spite of the depth of the fossa the internal margin does not extend very far onto the dorsal surface of the cranium and there is only a relatively small and poorly-defined depression around its inner edge, while

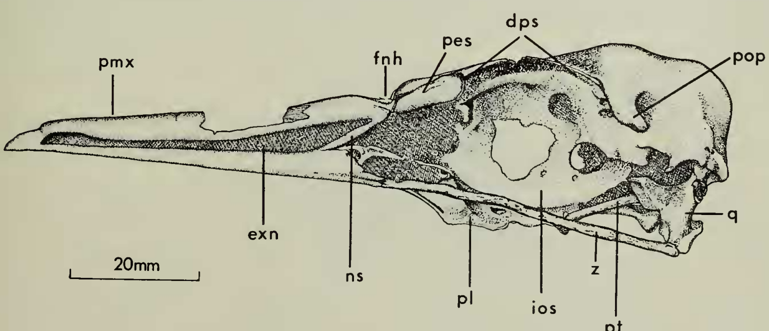

FIG. 2. Left lateral view of skull, × 1. Abbreviations as in Fig. 1.

posteriorly the main fossa slopes back to the line of the fronto-parietal junction. The fronto-parietal edge is superficially eroded and the original temporal fossa may have been more clearly defined.

Posterior to the fossa the squamosal and parietal form an arch over the auditory meatus with a slight peak marking the posterior edge of the fossa ; the quadrate articulates immediately below it. On the left side the outer edges of the bones are damaged, while on the right side both the postorbital process and the region above the quadrate are broken.

The cranium is rather small and projects forward medially with the result that, within the orbit, the posterior part of the frontal which forms the anterior ventral wall of the cranial cavity slants away postero-laterally, and also at an angle of *c.* 45° postero-ventrally.

In the upper region of the orbit the frontal is pierced, on either side of the interorbital septum, by a large oval fenestra opening into the cranial cavity. At the lower posterior edge of the frontal (or possibly in the orbitosphenoid) there is a large optic foramen, piercing the interorbital septum and extending laterally on either side of it. The septum itself is fragmentary and shows an extensive irregular central fenestra and various small subsidiary foramina. There are grooves, presumably to accommodate nerves, along the dorsal and ventral edges of the septum. The interorbital region of the frontal is thick, the roof of the orbit sloping from the orbit edge towards the septum.

At its anterior dorsal end the interorbital septum is pierced by a small, vertical fenestra which extends up into a hollow in the ventral surface of the frontal at this point. Just posterior to this fenestra the septum edge forms a thickened ridge descending from the orbit roof and curving forward below the fenestra, becoming concealed by the matrix which encloses the inner nasal region. The interorbital fenestra and hollow may have accommodated some structure with an olfactory function. This area is more complete on the left side of the specimen.

On this side the roof of the orbit shows a peculiar feature. Within the orbit, along its dorsal edge, there is an elongated oval depression, extending slightly inwards and terminating internally at an abrupt ridge where the frontal resumes its normal thickness. It is not clear to what extent the edge of the orbit may have been damaged, but there has been a reduction in thickness of the orbit roof, towards its edge, to accommodate a structure which was elongated, broader towards its middle, and dorso-ventrally flattened to an even thickness.

At the anterior end of the orbit the frontal is thick and abruptly flattened on the lateral surface. In some of the Recent Pelecaniformes this condition is associated with the presence of a closely attached but unfused prefrontal, which may fall away to reveal a similar surface of attachment. It therefore seems likely that a projecting prefrontal was originally present in *Prophaethon*, but has been lost. On the left side, within the orbit, there is an incomplete and laterally projecting flange of bone at the middle of the anterior edge of the interorbital septum. This might be the remains of the lateral ethmoid plate associated with it. In either case there is evidence for the existence of some structure at the anterior end of the orbital cavity, of a type normally associated with a prefrontal.

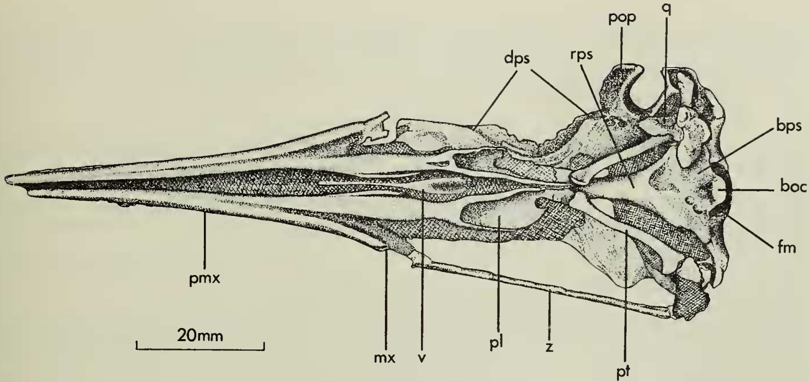

FIG. 3. Ventral view of skull with left zygoma removed, × 1. Abbreviations as in Fig. 1.

The jugal and quadratojugal form a narrow even strut of bone arising a little dorsal to the posterior tip of the maxillary and extending in a straight line back to the quadrate, continuing the line of the tomium of the upper mandible. The bar has been fragmented but appears to be laterally flattened along its entire length and shows no torsion.

Ventrally (Fig. 3 ; Pl. 1, fig. B), the basiparasphenoid is a small and triangular plate, tapering anteriorly to a smooth rostroparasphenoid and at the external posterior corners curving ventrally to form a pair of blunt projections only a little anterior to the occipital condyle. The area is damaged and pitted in places and it is not possible to be certain of the structure of the anterior part of the basiparasphenoid plate.

The posterior surface (Fig. 4 ; Pl. 1, fig. E) of the cranium is rather flattened, but a little inflated in the region of the supraoccipital. The foramen magnum is large and rounded and tilted slightly downwards. The parietals form a broad arch over the foramen. They are slightly hollowed dorsally towards the inner end, and the

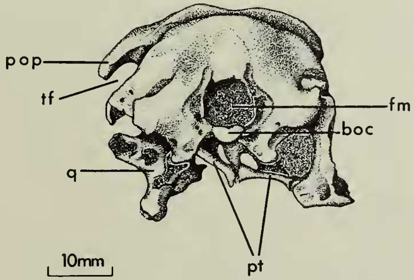

FIG. 4. Posterior view of skull, × 1. Abbreviations as in Fig. 1.

outer ventral edges are prominent and rounded posteriorly. The surfaces of the exoccipitals are concave. They have a slightly anterior ventral slant and begin to taper ventrally before expanding again at the line of fusion with the posterior edge of the basiparasphenoid plate.

Quadrate. In *Prophaethon* the right quadrate is in the normal position with the shaft vertical, but it has been damaged along its external side. The left quadrate is also in position, but the posterior end of the pterygoid has become displaced upwards, allowing the quadrate to tilt inwards at its lower end ; it is held in this position by matrix on the internal side. The tilt has displaced the dorsal articulating surface and allows a better view of this end.

The shaft is postero-anteriorly flattened, the narrow waist at the level of the orbital process being about three times as broad as it is thick, and widening towards the dorsal and ventral ends. The dorsal head is laterally broad, the external flange of the otic process projecting laterally as far as does the quadratojugal socket on the ventral head. The otic process slants laterally from the waist to form a rather flattened process, with a shallow ridge from the base of the orbital process crossing the anterior surface, but with some of the posterior surface and tip broken away. The internal facet of the dorsal head appears to terminate as a rounded structure projecting internally only a little further than the inner edge of the shaft.

The orbital process is blade-like, with an almost horizontal upper edge and a slightly rounded tip. From this tip it curves down towards the lower part of the shaft. It appears to project anteriorly at an angle to the quadrate shaft of about 70°.

The ventral head of the quadrate is elongated laterally. The quadratojugal socket projects laterally and curves forwards so that the entrance of the socket is more anterior than the lateral alignment. The posterior side of the head curves back from the articulation socket to form a projecting posterior flange ; from the posterior side of the broken right quadrate of the specimen it would appear that there is a fairly deep but small groove on the lower end of the mid-shaft, cutting into the flange. The ventral surface of the quadrate then curves anteriorly again, but on the specimen the mandibular articulation surface of this region is damaged.

Palate (Fig. 3 ; Pl. 1, fig. B). The skull presents an example of a typical schizognathous palate. The maxillae are broadest posteriorly at the point where they fuse with the palatines, and posteriorly they then taper rapidly on the external side to the articulation with the jugal. Anteriorly, they taper a little and extend for most of the length of the rostrum with a narrowing gap between them, fusion presumably occurring in the premaxillary region at the tip of the rostrum (now lost). They are slightly hollowed ventrally and the external edge projects ventrally to form the tomium of the upper mandible. The palatines arise near the posterior ends of the maxillae and extend back as shafts of similar width to the maxillae, but tapering a little, and then expanding in the region below the orbits, to form elongated, ventrally-hollowed blades, their posterior ends articulating with the pterygoids. The posterior external sides of both blades are a little broken but together they show the line of the external and posterior edge.

The palato-maxillae arise on the internal edge of the palatines near the region where the latter diverge from the maxillae. They extend posteriorly as narrow blades lying alongside the internal edge of the palatines, but from the side view of the skull it can be seen that they are laterally flattened blades with the upper edges curving dorsally and externally on either side of the vomer. Laterally, in the angle between the nasal bars and the posterior end of the maxilla, this upper edge of the palato-maxilla can be seen on the right side of the specimen as a projecting flange level with the junction of the nasal and maxilla ; on the left side it is broken, revealing the narrow extensions where it joins the internal ventral and internal dorsal ends of the maxilla.

Dorsally, the internal edge of the palatines extends upwards on either side of the anterior ventral edge of the interorbital septum, its posterior edge curving inwards and downwards to meet the posterior dorsal surface of the vomer. This structure is fairly complete but a little broken along its upper edge on the left side, and more extensively broken, but still showing curvature, on the right side.

The pterygoids are slender shafts. In ventral and lateral view the anterior end which articulates with the posterior tip of the palatine can be seen to be expanded, the sides diverging fairly evenly towards the tip on the ventral surface and with a prominent rounded dorso-external end visible laterally. The main shaft shows some lateral flattening and where it articulates with the right quadrate it shows dorso-external torsion and a rounded, blade-like expansion at the posterior dorsal end. This appears to increase the extent of the articulation with the internal side of the ventral end of the quadrate.

Rostrum. Where it joins the skull the rostrum is almost square in transverse section, but slightly narrower dorsally ; anteriorly it tapers very gradually to a point. The frontal region of the skull terminates in a bold ridge, bordered anteriorly by the deep, transverse fronto-nasal hinge. From the base of this ridge a rather flat nasal surface of the basal rostrum projects anteriorly, merging into the premaxilla, and tapering and becoming more rounded dorsally towards the anterior end. On either side it is separated from the more ventrally situated maxillae by an elongated aperture which also tapers and which extends to near the distal tip of the rostrum. Two slender bars of the nasal slope posteriorly upwards from the posterior part of the maxillae just where these widen, and appear to fuse laterally with the edges of the broad posterior rostral surface just anterior to the fronto-nasal groove.

Mandible (Fig. 6f ; Pl. 2, figs A–C). The mandibular rami are slender, elongated and with only a gradual taper towards the tip. They have been twisted and show a dorsal torsion to the right. The distal end is damaged but the more proximal and articular regions are complete. The dentary portion of each ramus is moderately rounded externally, more marked towards the ventral edge. The internal side of the dorsal edge slants ventro-laterally, and ventral to this a deep groove occupies the centre of the internal surface, extending along the distal two-fifths of the mandible. Proximal to this groove the internal surface is rounded with a more prominent central ridge, continuing the internal tomium edge and gradually descending

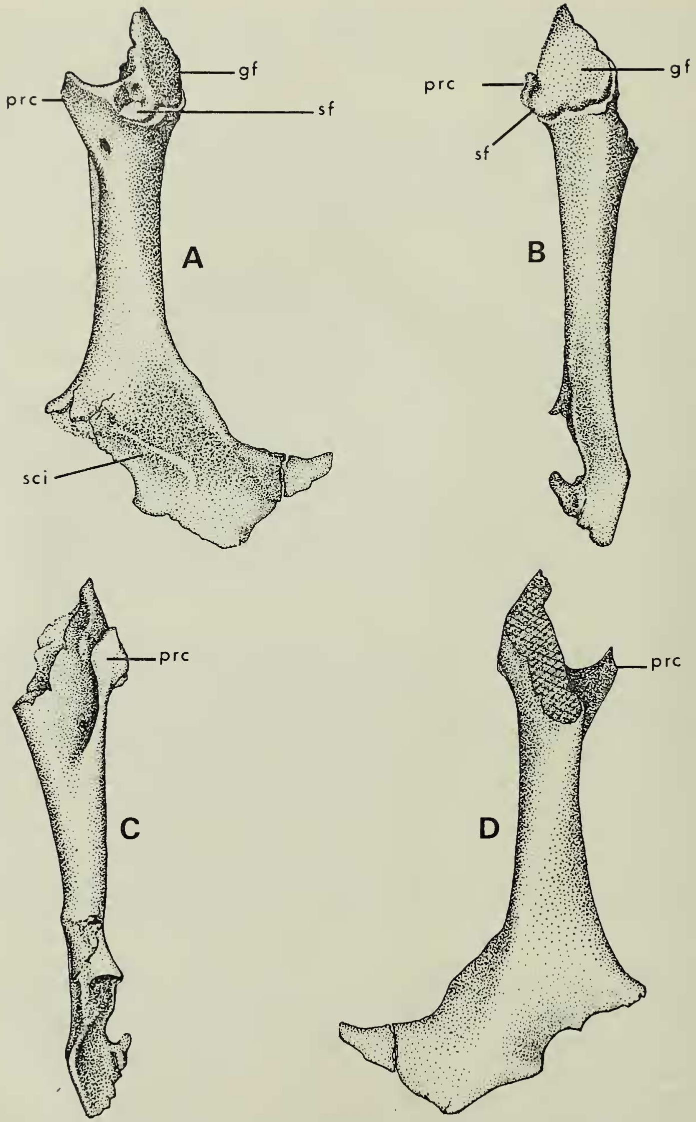

FIG. 5. Views of right coracoid, × 2. A, dorsal; B, external; C, internal; D, ventral. Abbreviations: gf, glenoid facet; prc, procoracoid; sci, sternocoracoidal impression; sf, sternal facet.

ventrally and becoming shallower, to disappear near the ventro-posteriorly slanting mandibular suture. On the internal side (Fig. 6f), the upper edge of the splenial extends about three-quarters of the way along the ventral anterior edge of the suture and then extends anteriorly and ventrally as a thin line.

The mandibular suture appears as a deep groove internally, and much of the lower half is occupied by a narrow, elongated fossa, at the anterior end of which a narrow slit forms the internal opening of a poorly-defined anterior mandibular fenestra. Externally (Pl. 2, fig. C) the upper part of the suture is fused, but there is a narrow, elongated fossa, the dentary edge ventral to it projecting slightly so that the fossa is internal to it rather than dorsal. The upper edge of the fossa forms an external opening for the fenestral slit. Posterior to this external fossa the suture extends back ventro-posteriorly between the dentary and the anterior ventral parts of the supra-angular and angular. From the anterior end of the fossa a shallow and broad but well-defined groove extends almost horizontally along the external face of the dentary and terminates at a level a little posterior to that of the posterior end of the groove on the internal face of the mandible.

On the broad, internal face of the posterior part of the mandible, towards the dorsal edge, there is a large, oval, posterior mandibular fossa between the pre-articular and supra-angular. Since this is filled with matrix the internal structure is not visible, but it does not penetrate to the external surface.

Posterior to this fossa the mandible becomes less deep, but broadens rapidly just before the surface of the articulation with the quadrate. Dorsally, the surface widens rapidly into a triangular, smooth surface with a small articular prominence at the external corner. On the posterior side of the surface is a deep hollow which articulates with the ventral head of the quadrate. It has a complete dorsal rim on the external side, but elsewhere slopes to a median groove which occupies the centre of an extension of the hollow opening into the internal side. Posterior to the hollow the dorsal surface terminates as a narrow edge, broadening at the internal end into a small triangular surface with a raised and rounded internal tip, and on the inner side of this, broadening the posterior edge of the hollow, there is a small rounded foramen.

The posterior surface of the mandible is flattened and forms a modified inverted triangle. It has a distinct and narrow dorso-internal protrusion, while the lowest part is more broadly rounded and projects as a narrow, curved lip beyond the main ventral shaft. The surface is hollowed at the centre. The true position of this surface is difficult to determine because of the torsion of the specimen, but it appears to show some internal deflection and a marked posterior-dorsal tilt, the ventral lip projecting beyond the rest of the structure.

b. *Postcranial elements*

STERNUM (Fig. 6a–c). The sternum was previously concealed within the matrix and its presence was not suspected until the present preparation had begun. It is still partially embedded in matrix and lacks its posterior end and the lateral posterior parts of the sternal plate. The carina, which lacks the posterior end, is exposed on its right side and along the anterior and ventral edges. In addition the

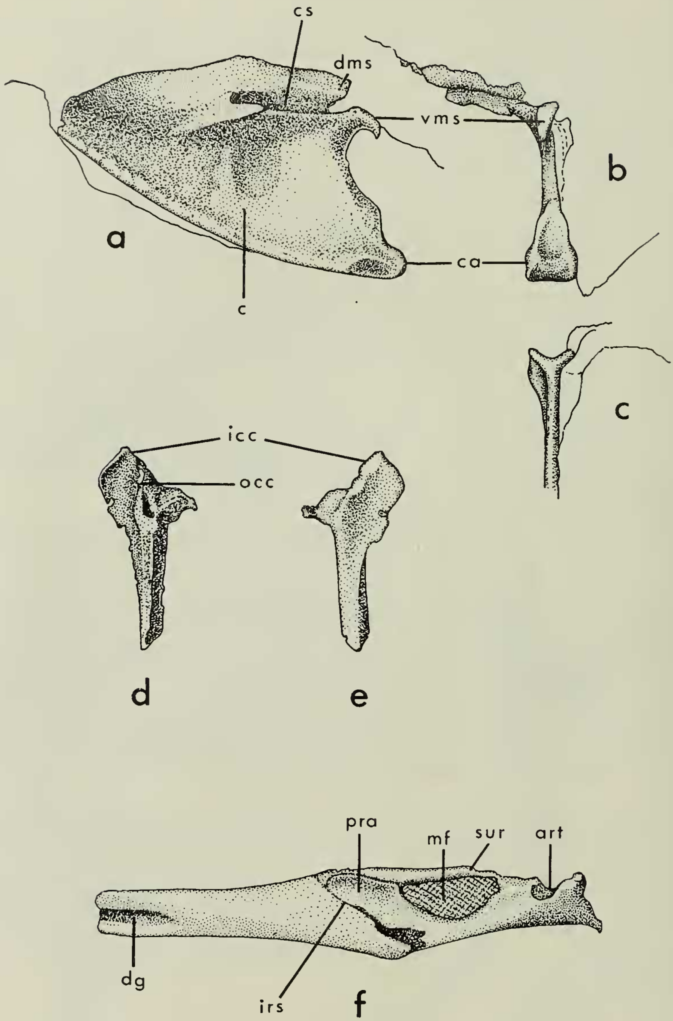

Fig. 6. Views of partly embedded sternum, × 1 ; a. right lateral, b. anterior, c. ventral. Views of imperfect left tibiotarsus, × 1 ; d. oblique anterior, e. oblique internal. f. View of the internal side of right mandible, × 1. Abbreviations : art, articular ; c, carina ; ca, carinal apex ; cs, coracoidal sulcus ; dg, dental groove ; dms, dorsal manubrial spine ; irs, inter-ramal suture ; mf, mandibular foramen ; occ, outer cnemial crest ; pra, prearticular ; sur, surangular ; vms, ventral manubrial spine.

ventral manubrial spine and right half of the manubrium and coracoid sulcus are also present. The right half of the sternal plate is shattered posterior to the thickened region of the sulcus and lacks the external and posterior parts.

The sternal plate shows slight ventral curvature. The carina is large, projecting ventrally and anteriorly, with a slight curvature of the ventral margin. It becomes thicker anteriorly, and at the carinal apex bifurcates to accommodate the ventral end of the anterior articulating surface. The anterior carinal margin is stout, but tapers at the dorsal end where it curves up to the underside of the ventral manubrial spine. The latter is a small sharp projection, an inverted triangle in transverse section with the wider dorsal surface rising slightly anteriorly and then curving forwards and downwards, tapering away to a point a little below the level of the ventral edge of the spine.

The anterior carinal margin curves forwards ventrally, its apex anterior to the tip of the spine. The upper part, about three-fifths of the whole, curves forwards and becomes thicker ventrally, and forms a blunt projection at a similar anterior level to the tip of the manubrial spine. Below this, the remaining two-fifths form a flattened, elongated anterior facet, hollowed centrally and curving forward ventrally. It appears analogous to similar surfaces on the sterna of some pelecaniform species, which articulate with the furcula in the region of the ventral symphysis. Viewed laterally (Fig. 6a), this surface on *Prophaethon* is hollowed to such an extent that it shows some posterior curvature. Viewed anteriorly (Fig. 6b) it is dorso-ventrally elongated and wedge-shaped, widening ventrally and with the ventral portion curving anteriorly. At the ventral end the hollow becomes shallower, forming a poorly-defined lip below the deepest part of the cavity.

The dorsal lip of the coracoid sulcus appears thickened but is superficially damaged. The ventral lip arises at the lateral dorsal edge of the base of the ventral manubrial spine and slants posteriorly across the sternal plate. There is a broad ventral surface between the anterior edges of the dorsal and ventral lips. The ventral labial prominence occurs about two-thirds of the way along the sulcus as a bluntly rounded, thin flange overlapping the sulcus which up to this point appears to be ventrally exposed. A low ridge across the sternal plate from the posterior part of the carina terminates at the sulcus after crossing the ventral surface of the ventral labial prominence.

The sulcus terminates a little lateral to the prominence, the ventrally projecting ridge of the dorsal lip curving posteriorly towards the end of the sulcus to leave a thinner, laterally-projecting, area of the sterno-coracoid impression.

Coracoid (Fig. 5 ; Pl. 2, figs D–G). The right coracoid is preserved, but anteriorly it is broken off just above the glenoid facet, the broken surface extending along part of the ventral edge. The sterno-coracoid process and internal distal angle are also damaged.

The shaft is smooth and rounded, but towards the distal (sternal) end it is dorso-ventrally flattened. The sterno-coracoid surface is large and slightly curved ventrally, and since the dorsal lip of the coracoid sulcus is markedly anterior to the ventral lip, as already described in discussing the sternum, the ridge marking the articulating surface for the latter appears across the middle of the dorsal surface of the sterno-coracoid area. It becomes lower and disappears before reaching the flattened and rather rectangular sterno-coracoid process. The internal distal angle of the coracoid is broken off at the line of the articulation ridge.

The shaft becomes thicker and more rounded, and laterally narrower, as it approaches the procoracoid. From the faint scar of attachment of the coraco-brachialis a poorly-defined ridge crosses the shaft to the distal end of the procoracoid. The latter projects laterally and curves anteriorly and ventrally to a point (broken short in the specimen). On the internal side there is a curved hollow between the procoracoid and shaft, with a small longitudinal ridge on either side of it. The internal opening of the coracoid fenestra is a small hole near the distal end of this hollow, and the external opening is a similar hole on the dorsal surface of the procoracoid, towards its edge.

The scapular facet is shallow and dorsal, and from it a thickened ridge borders the proximal edge of the procoracoid. The glenoid facet is dorsoventrally aligned. Ventrally, there is a low ridge from the ventro-external edge of the shaft, which crosses the sterno-coracoid process and terminates near its distal external extremity.

Scapula. The single left scapula lacks the proximal articulating end. It is a slender rod with a slight ventral curvature, dorso-ventrally flattened. It is a little thicker and more rounded at its base and towards its tip becomes more flattened and broader, then tapers to a point.

Pelvis (Pl. 3, figs A–C). Most of the pelvis is present. At the anterior end of it a row of laterally crushed vertebrae form the relic of the thoracic part of the vertebral column. Dorsally the pelvis has been cleared of matrix but some of the more ventral detail of the left side is still obscured by matrix containing broken ribs. On the right side it is completely exposed. The anterior lateral edge of the ilium is broken on the right, but appears complete on the left side. Posteriorly, on the right, the ischium and pubis are broken off at about the posterior end of the ilio-ischiatic fenestra, and the ilium posterior to the fenestra is also missing, the dorsal end terminating at the incomplete caudal end of the synsacrum. On the left side, part of the iliac portion of the synsacrum is visible and the ventral struts of the roof of the renal depression can also be seen on the left.

At the anterior end of the pelvis the median-dorsal ridge is thick and prominent, appearing to fuse with the end of a row of elongated and flattened neural spines. The ridge projects sharply, the iliac plates sloping down steeply on either side and curving outwards to form a lateral flange, broadest anteriorly and with a rounded tip. Posteriorly the dorsal ridge widens and the iliac plates become narrower and less hollowed laterally. The edges of the ridge diverge as two well-defined edges of the anterior iliac crest, curving outwards to a slight prominence above and internal to the acetabulum. From there, two blunt, broad ridges continue posteriorly as the posterior iliac crest, curving slightly towards each other in the region of the ilio-ischiatic fenestra, before diverging posteriorly. The shield area between them is narrow and slightly hollowed, with a median ridge beginning to appear towards the posterior end ; on the left side at the posterior end there is what may have been the first of a double row of narrow fenestrae from the renal depression. Below the posterior iliac crests the iliac surface slopes outwards as a narrow upper edge to the iliac-ischiatic fenestra. The fenestra is large and elongated, becoming wider posteriorly, with a relatively straight lower edge, a posteriorly-curved upper edge, and the two meeting anteriorly in a small rounded end just posterior to the lower edge of the antitrochanter. Anteriorly the surface bordering the upper edge of the fenestra flares out to a prominent lip over an antitrochanter, the articulating surface of which has an anterior/external aspect and also an anterior/ventral slant. Below this is a rounded acetabulum, the lower third of which does not penetrate completely to the ventral side, but forms a rounded hollow in the bone. There is a small lateral projection midway along the anterior external edge of the acetabulum.

Just ventral to the anterior edge of the acetabulum a small anteriorly-projecting pectinal process is present, posterior to which the pubis slopes away as a slender rod of bone. The anterior end of the ischio-pubic fenestra is narrow but rounded and terminates posterior to the ventral edge of the acetabulum. Dorsal to it the ischial bar is nearly twice the width of the pubis. Just posterior to the acetabulum the external surface of this ischial bar slopes ventro-internally, until it meets a small ridge which slopes back from the posterior edge of the antitrochanter, at which point torsion occurs and the external face of the ischium has a ventro-external slant, and shows a poorly-defined, posteriorly and ventrally slanting, ridge in its surface.

The fused synsacrum has its greatest depth at the anterior end and viewed laterally the dorsal line of the pelvis and the ventral surface of the synsacrum converge towards the posterior end, forming a thin elongated wedge that shows a slight ventral curvature at its posterior tip. The ventral surface of the synsacrum is widest at the region of the sacral vertebrae, where it shows a well-defined median groove, and tapers gradually towards the posterior end. Anteriorly it also begins to taper but becomes broader again at the anterior tip where it articulates with the first free vertebra. The latter appears to be the last dorsal vertebra. The anterior articulation surface of the synsacrum is posterior to the broad dorsal anterior edge of the ilium.

FEMUR. The right femur was exposed in the specimen as originally prepared ; it appears from the original figure (Andrews 1899) to have had a coating of matrix and to have been superficially damaged beneath this. The present preparation has exposed on the distal half, which is detached from the main block but still attached to the tibiotarsus, an internal distal surface almost to the condyle ; on the proximal half still *in situ* on the pelvis the external and posterior surfaces are visible.

The distal internal face shows a smooth, slightly rounded surface with a rounded and posteriorly projecting condyle, the internal condylar surface showing an internal deflection towards the distal end.

The trochanter shows an abrupt obturator ridge with a hollow beneath it on the posterior side. The anterior head of the trochanter is rounded, and the external edge appears to form a blunt, projecting ridge which extends for some way along the anterior external edge of the shaft.

Tibiotarsus (Fig. 6d–e ; Pl. 3, figs D–E). During preparation the proximal end of the left tibiotarsus was removed and cleaned. The external side of the shaft had originally broken away as far as the head, but the internal side is still intact.

The anterior and internal sides of the shaft are present and where they join there is an abrupt edge which becomes more prominent towards the proximal end and finally forms the anteriorly-projecting flange of the inner cnemial crest. The inner cnemial crest is a thin prominent flange arising along the internal edge, projecting anteriorly and at its outer edge curving a little externally. It extends proximally well beyond the articulating surfaces. It arises gradually from the shaft, is deepest at about the level of the proximal edge of the articulating surfaces, and then tapers to a blunt point proximally. The outer cnemial crest arises on the anterior surface near the external edge and nearer the proximal end than does the inner crest. It is thicker distally than the inner cnemial crest and projects at an angle between the anterior and external surfaces, curving slightly towards the external side. Its proximal end terminates at an angle a little proximal to the articulation surfaces. It appears to end abruptly as though broken short but this is also apparent on some entire examples of Recent species.

The internal articular surface is more distally placed than the inter-articular area and the ends of the crests. Its surface is damaged on the specimen, but it shows a posteriorly-projecting, curved lip. The inter-articular area slopes distally on the external side, curving distally to the broken external surface in a shallow hollow on the external side of the outer cnemial crest.

Ribs and other elements. The head of a rib and part of another are visible on the left side of the specimen anterior to the pelvis, together with broken shafts still embedded in matrix. The visible head is relatively stout ventral to the tubercle, and the portions of shaft are fairly broad. There is no obvious uncinate process, but a slender and flat strip of partially embedded bone parallel to the left posterior iliac crest might be referable to this. In general structure the ribs resemble those of the larger larids and sulids.

In addition to the material described above, there are also a number of fragments of bone and matrix removed during preparation. A close examination of these might make their identification possible, but they are not likely to provide additional useful information to the present study. Their existence is therefore noted, but no further study has been made.

c. *Measurements*

All dimensions are given in millimetres.

Skull

Overall length (premaxilla–supraoccipital)	112
Maximum width at posterior end (squamosals)	35·5
Maximum width at postorbital processes	38
Minimum width of interorbital bar	15
Width at anterior end of frontals	16·7

Skull (continued)

Width at base of rostrum (dorsal)	15·8
Width at base of rostrum (ventral)	20
Mid-rostral width	10
Width at tip of rostrum as preserved	3·8
Length of culmen	61
Length of lateral nasal aperture	50·4
Maximum depth of lateral nasal aperture	3·4
Posterior depth of cranium to occipital condyle	19·5
Maximum cranial depth	24.5
Depth from anterior end of frontals to palatines	19·9
Width of temporal fossa at postorbital process	6·1
Minimum width of cranium at temporal fossae	26
Length of dorsal hollow in orbit (? nasal gland)	22
Width of dorsal hollow in orbit (estimated)	4
Length of palatines	42
Maximum proximal width of palatines	5·6
Length of pterygoid	1·8
Width of shaft of pterygoid	1·6
Width at quadrato-pterygoid articulation	4·3
Maximum width of posterior end of basiparasphenoid plate	17
Width of rostroparasphenoid	3·2
Length of zygoma	44·2
Depth of zygoma	2·6
Width of zygoma	1·3

Quadrate

Quadratojugal socket to otic process	14·5
External–internal width of quadrato-articular surface	12
Anterior–posterior width of quadrato-articular surface	5·9
External–internal thickness of shaft below orbital process	4·8
Maximum depth of orbital process	6·2
Length of orbital process	7·8

Lower Mandible

Maximum length of left dentary to post-articular process (incomplete)	109·9
Maximum length of right dentary to post articular process (incomplete)	112·2
Depth of dentary at tip	4
Width of dentary at tip	1·9
Depth of dentary at proximal end of internal dentary groove	6·7
Width of dentary at proximal end of internal dentary groove	3·7
Maximum depth of dentary at intra-ramal suture	13·2
Maximum width of dentary at intra-ramal suture	2·3
Depth at anterior end of articular surface	6·5
Width at anterior end of articular surface	9·1
Depth at posterior end of articular surface	9·3
Width at posterior end of articular surface	11·2
Maximum length of posterior mandibular fossa	14·3
Maximum depth of posterior mandibular fossa	6·7

Scapula

Overall length (incomplete)	67·7
Maximum distal width	6·2
Proximal width	4·9
Thickness at proximal end	2·7

Coracoid

Overall length	43·2
Maximum distal width	19·9
Width of glenoid facet	6·1
Width of scapula facet	2·1
Width of sternal facet	5
Width of shaft at coracoidal fenestra	6·8
Internal–external length at sternal facet (left)	20·2
Proximodistal width of sternocoracoidal process (left)	8·5

Sternum

Maximum length to ventral manubrial spine	51·5
Length of carinal edge (incomplete)	59
Carinal apex to dorsal edge of ventral manubrial spine	26·5
Tip of ventral manubrial spine to anterior carinal margin	6·3
Length of furcular facet	10·9
Maximum width of furcular facet	6·8
Tip of ventral manubrial spine to ventral labial prominence	22·1
Width of coracoidal sulcus	5·7

Pelvis

Maximum medial length as preserved	67
Anterior border of ilium to anterior edge of acetabulum	35
Maximum width across antitrochanters	27·4
Anterior width from external edge of ilium to medial ridge	17
Length of ilio-ischiatic fenestra	23·3
Maximum depth of ilio-ischiatic fenestra	10
Minimum distance between antitrochanter and pectineal process	14
Ventral length of synsacrum	69·5
Anterior depth of pelvis from median dorsal ridge to synsacral thoracic vertebra	19·5
Width of articular facet of first synsacral thoracic vertebra	7·5

Femur

Proximodistal length	51
Anterior/posterior thickness at midshaft	4·8
Maximum proximal width at trochanteric ridge	9·4

Tibiotarsus

Length as preserved	31·3
Articular surface to tip of internal cnemial crest	6·1
Maximum width of internal cnemial crest	5·2
Width from internal edge to external edge of internal cnemial crest	15·5
Width to internal edge of internal cnemial crest	8·6
Width to external edge of outer cnemial crest	14

III. COMPARISONS WITH RECENT MATERIAL

In attempting to place *Prophaethon* within the framework of avian taxonomy, using the characters revealed by further preparation, it has been necessary to compare it with osteological material from various Recent taxa. Since the earlier claims of pelecaniform similarities were based on skull characters it seemed preferable for comparative purposes to begin at the other extremity.

Proximal end of Tibiotarsus. The obvious characters on this element are the prominent inner cnemial crest, which has its widest part just above the level of the articulation surfaces and tapers proximally, and the inner cnemial crest forming a blunt projection at a similar level. The proximal articular surface slopes posteriorly and has a projecting lip with a concave proximal surface at the posterior edge. The external edge of the proximal surface curves smoothly over onto the shaft in a broad zone where it borders the inner cnemial crest.

Stercorarius provides a very close match in all aspects, while other Charadriiformes also show resemblance to varying degrees. In the Procellariiformes *Diomedea* shows some similarities but lacks the projecting posterior lip, and has a larger and more proximally situated inner cnemial crest. There is no obvious resemblance to the Pelecaniformes, where *Phalacrocorax* retains only a short curved outer cnemial crest while *Sula* has small blunt projections. The features are almost entirely lacking in other pelecaniform genera.

Femur. This is long and narrow, the trochanteric crest present as a prominent narrow ridge rounded off at the proximal end with a curved muscle scar incised into the external surface. In the Charadriiformes the ridge is much more developed, both anteriorly and proximally. *Macronectes* in the Procellariiformes shows similarities to the specimen. *Sula* has a stout, curved femur, the proximal end of which shows some similarity to that of *Prophaethon*, but the trochanteric ridge is low and blunt and the head is more ventrally deflected.

Pelvis. The narrow, elongated pelvis is typical of that found today in birds which swim and dive to catch their prey. It bears no resemblance to that of *Phaëthon*, which is broad and short.

The anterior shield of the ilium extends forward only as far as the proximal end of the second synsacral thoracic vertebra, and the third vertebra is unfused. This condition is typical of the Charadriiformes but not of the other orders examined here. *Sula* does, however, show a short anterior iliac shield.

The median dorsal ridge is slightly convex, but posteriorly it is depressed between well-defined posterior iliac crests. In this respect the specimen resembles *Phoebetria*, *Diomedea* and *Puffinus* among the Procellariiformes. The Alcidae show a similar profile. In the Pelecaniformes the posterior iliac crests are poorly developed and in the more aquatic forms such as *Sula* and *Phalacrocorax* the posterior median ridge is level with or dorsal to the lateral crests.

The Pelecaniformes also show more laterally projecting and anteriorly directed antitrochanteric surfaces than does *Prophaethon*, and in the latter the iliac surface immediately anterior to the acetabulum is concave and the pectineal process prominent. The specimen is more similar in these respects to both Procellariiformes and Charadriiformes, although among the last the Alcidae show the pectineal process greatly reduced or absent. From fine sutures apparent on the specimen the ilium would appear not to have been fused with the synsacrum, in this respect resembling Recent Alcidae and Procellariiformes rather than Pelecaniformes.

Vertebrae. The free thoracic vertebrae appear to lack hypopophyses. They have rounded concavities laterally, posterior to the prominent anterior costal facet. The diapophyses are short, dorsally broad and have a thin middle ridge ventrally with a deep concavity at the internal corner of the anterior side. There is a thin, tapering anterior process at the distal end of the diapophysis. These vertebrae resembles those of the larger *Larus* species in the Charadriiformes. Those of the Procellariiformes are more elaborate with larger concavities and various fenestrae, and with hypopophyses ; those of the Pelecaniformes show still fewer similarities to those of *Prophaethon*.

Sternum. Allowing for the incompleteness of the specimen the carina of the sternum is deep and long, extending further back than is the case on Recent Pelecaniformes. The ventral lip of the coracoid sulcus is posteriorly situated so that the sulcus is ventrally exposed, particularly at the middle region, but towards the outer end it undercuts a small but broad labial prominence.

In the Pelecaniformes the ventral lip of the sulcus extends almost as far anteriorly as does the dorsal lip, and the sulcus is a deep, anteriorly-directed groove. In *Prophaethon* the groove is more typical of that found in Charadriiformes and Procellariiformes. From the ventral labial prominence a distinct intermuscular line slants postero-internally towards the middle of the carina. A similar line is present in Charadriiformes, but in the Procellariiformes one line arises on the sulcus internal to the labial prominence and crosses the sternum more anteriorly, while another rises towards the external end and slants towards the posterior end of the carina. In Pelecaniformes there is a faint ridge from the labial prominence apparent in Phalacrocoracidae and Phaethontidae.

The hollow facet for furcular articulation at the anterior tip of the carina is a distinctive character in *Prophaethon*. Structures of this kind are found in some Recent species of Pelecaniformes and Procellariiformes. A small articulation surface is present on the larger Podicipitiformes. This furcular surface is more extensively developed in the Pelecaniformes where the Pelecanidae and Fregatidae have the furculum fused to the sternum while Phaethontidae, Sulidae and Phalacrocoracidae have the surface developed to varying degrees. Of the Procellariiformes the Pelecanoididae have a sternum with a large furcular articulation facet, its ventral edge curved anteriorly. The bifurcation of the carina tip, apparent in *Prophaethon*, is characteristic of many Procellariiformes but not of the Pelecaniformes. None of the Charadriiformes show furcular articulation facets on the sternum.

The shape of the manubrial spine in *Prophaethon* resembles that of *Phaethon*, but this structure differs so markedly in different families and genera that we do not regard it as taxonomically useful.

Coracoid. The shape of the sternal (distal) end of the coracoid is correlated with that of the coracoid sulcus. The coracoids of Pelecaniformes show sternal facets on both sides at the distal end, articulating with the deep sulcus. *Prophaethon* resembles charadriiform and pelecaniform birds in having a prominent facet across most of the dorsal surface ; a small one on the ventral surface towards the external end is correlated with the position of the ventral labial prominence of the sternum. From the fit of the specimen there is no reason to suppose that the missing internal distal angle of the coracoid of *Prophaethon* would have projected across the midline of the sternum, as in *Phaethon*.

A stout and dorsally curved internal distal angle to the coracoid is characteristic of most Procellariiformes, although less evident in the Pelecanoididae, and in the Laridae and Alcidae of the Charadriiformes. Although this part of the specimen of *Prophaethon* is damaged, the general shape of the surrounding bone and the sternal fragment of the other coracoid, which is also present, indicates an absence of such curvature. The specimen most closely resembles the flatter coracoids of *Ibidorhynchus* and *Haematopus* of the Charadriiformes in this respect ; it also resembles them in the area of irregular surface on the dorsal side distal to the line of attachment of the coraco-brachialis muscle, the proportions of the shaft, the procoracoid, and the position of the coracoidal fenestra.

LOWER MANDIBLE. This, although relatively complete, does not give an indication of affinity with any particular taxon.

The slender ramus, increasing in depth posteriorly and tapering a little at the anterior end of the articular portion, has a general resemblance to those of Phalacrocoracidae and some Procellariidae. The tapering groove on the external surface anterior to the intraramal suture is similar to that of Procellariiformes and Charadriiformes, but a groove of this type is also present in *Phaethon*.

The arrangement of the component bones around the external fossa of the mandibular suture and the shape and position of the fossa itself are most closely paralleled by the structure in some smaller Laridae, the Burhinidae and to a lesser degree by some Procellariiformes. The concave, ventrally tapering and postero-dorsally oriented postarticular surface is very similar to that of Gaviiformes, but only resembles to a limited extent those of the other taxa examined here.

The articular facets are very similar to those of Laridae, Burhinidae and Procellariidae but do not closely resemble the more specialized structures of the Pelecaniformes.

Prophaethon has a large, rounded posterior mandibular fossa, bordered anteriorly by a large prearticular which extends anteriorly to border the mandibular suture and overlaps with, and possibly fuses with, the dentary towards the dorsal edge of the ramus. This large prearticular is also present in the Procellariiformes and Gaviiformes. The Charadriiformes have a large posterior fossa but the prearticular is small and only partially occupies the anterior space, the mandibular slit forming a distinct fenestra. *Phaethon* shows a similar condition but has the prearticular larger posteriorly, reducing the size of the posterior fossa. In the other pelecaniform families the posterior fossa is tiny and the prearticular has filled the remaining space.

SKULL. The palate is typically schizognathous and resembles those of Charadriiformes and Gaviiformes. Procellariiformes also have this type of palate, but the distal end is modified by bill shape. The palates of Pelecaniformes appear to be schizognathous in the very juvenile condition but desmognathous in the adults. Schizognathous palates are also present in Podicipitiformes, Gruiformes, Galliformes, Sphenisciformes and Columbiformes. The distinctive proximal bifurcation of the vomer, visible between the palatines in *Prophaethon*, is very similar to that of larger *Larus* species and of other Charadriiformes, but does not appear in Pelecaniformes and Procellariiformes.

The rostrum of *Prophaethon* is long, slender and tapering. An elongated nasal aperture runs for almost the whole length, rising posteriorly and tapering to a slit just proximal to the frontonasal hinge. In general shape the rostrum is similar to that of the Phalacrocoracidae, and if it were argued that the latter retained the open aperture of the juvenile there would be strong similarity. In other Recent birds the elongated nasal apertures are typical of Charadriiformes, Gaviiformes, Podicipitiformes and Gruiformes. Although the nares of Pelecaniformes are typically closed or minute, *Phaethon* shows an intermediate condition with a short but relatively large aperture about a third of the way along the rostrum and a tiny hole near the frontonasal hinge.

A transverse frontonasal hinge developed to differing degrees in different families is associated with the greatly reduced nostrils in Pelecaniformes. In *Prophaethon* the nasal apertures are schizorhinal in shape, but since the nasal struts join the rostrum anterior to the frontonasal hinge they are functionally holorhinal. A holorhinal type of nostril associated with a frontonasal hinge in this position also occurs in the Charadriiformes in the Burhinidae, Thinicoridae and *Pluvianus* of the Glareolidae, although charadriiform nostrils are usually collectively described as schizorhinal. A deep transverse frontonasal hinge comparable with that of the Phaethontidae also occurs in *Rhynchops* of the Charadriiformes, but in this instance the nostrils are schizorhinal. Procellariiformes have an unspecialized transverse frontonasal structure and holorhinal nostrils.

In the Pelecaniformes the heavy frontal brow associated with a deep frontonasal groove is present only in the Phaethontidae. In the Charadriiformes it is partially developed in *Rhynchops*, and more highly developed in the Chionidae. In the latter the nasal struts lie alongside the rostrum and also terminate just below this brow, apparently forming a hinge with the rostrum. This structure has some analogy with that of *Prophaethon* since a close inspection of the latter reveals that the nasal lies close alongside the dorsal rostral surface but may not fuse with it completely, and the transverse line of the frontal brow is not completely straight but shows paired lateral recesses in the fore-edge which might be comparable with those of Chionidae. Unfortunately the surfaces of the bone are slightly damaged at this point in the specimen of *Prophaethon*.

The frontal shows a flattened lateral surface suggesting the loss of an unfused prefrontal. Prefrontals are unfused in the Phaethontidae and Fregatidae of the Pelecaniformes, and in Burhinidae of the Charadriiformes; when they become detached they leave flat surfaces similar to those of *Prophaethon*.

The smooth dorsal surface of the skull of *Prophaethon* may have pelecaniform similarities, but only by virtue of the absence of the nasal glands, and were these not present in other taxa they might also be similar. The feature is therefore a generalized one, indicative of absence of specialization rather than affinity. In the deeply rounded temporal fossae posterior to the prominently curved postorbital process the specimen resembles the Fregatidae, *Uria* of the Alcidae and *Stercorarius* in the Laridae, rather than the Phaethontidae, but shows some similarity to the last in the rather limited development of the fossae dorsally and anteriorly.

In the area of quadrate articulation the ventral edge of the orbitosphenoid curves forwards, leaving a large cavity anterior and internal to the articulation surface and tending to divide the latter into two. This is also present to a similar degree in the Pelecaniformes, but much reduced in the Procellariiformes and Charadriiformes.

The posterior aspect of the skull of *Prophaethon* has parallels in all the major taxa here examined, and there are considerable differences in these at the family level. The supraoccipital of *Prophaethon* has a small foramen on either side towards the ventral edge, with associated grooves bordering the upper edge of the foramen magnum. Similar structures are apparent in the Procellariiformes, more modified in the Charadriiformes, and greatly modified or absent in the Pelecaniformes.

Within the orbit of *Prophaethon* the hollow apparently accommodating the nasal gland is in a unique position, being an elongated hollow bordering the dorsal edge of the orbit and on the ventral surface of it. In Pelecaniformes the nasal gland is usually towards the anterior dorsal end of the orbital hollow and in a more median position. In some *Phaethon* species a small elongated hollow extends posteriorly into the orbit from this anterior site, bordering the orbital septum but separated from it by the channel of the olfactory nerve. In the Sulidae it is an elongated hollow lying completely in the roof of the orbit, but still close to the septum. In Charadriiformes and Procellariiformes the nasal gland hollow either borders the dorsal edge of the orbit or lies internal to it, but on the dorsal surface of the frontal. The position of this structure in *Prophaethon* is therefore intermediate between that in the two Recent types.

The slender, unspecialized pterygoids of *Prophaethon*, with a small posterior lateral expansion of the orbital process of the quadrate, give little useful evidence of affinity. The Phaethontidae show an even less modified structure, but the pterygoids of other pelecaniform families and of the other taxa discussed here are stouter, with some development of lateral flanges on the shaft, and in several diverse taxa show the expanded posterior end.

The quadrate of *Prophaethon* also shows little evidence of affinities, and the deep groove at the ventral end of the posterior surface of the shaft appears to be a peculiarity of the species.

Tables 1 and 2 give a simplified summary of apparent similarities. Tables such as this may oversimplify, exaggerating both similarities and differences, but they indicate the problem involved in assigning *Prophaethon* to a known taxon.

TABLE 1

Comparison of postcranial elements of *Prophaethon* with extant orders of birds

	Charadriiformes	Procellariiformes	Pelecaniformes
Proximal end, tibiotarsus	*	×	–
Proximal end, femur	–	×	×
Pelvis	*	*	×
Vertebrae	*	×	–
Sternum, other than anterior facet	*	×	–
Anterior edge of carina	–	*	*
Coracoid	*	*	×

* very similar; × some similarity; – little or no similarity

TABLE 2

Comparison of cranial elements of *Prophaethon* with extant orders of birds

	Charadrii-formes	Procellarii-formes	Phaethon-tidae	other Pelecani-formes
LOWER MANDIBLE				
Shape	×	*	–	*
External intraramal suture area	*	*	×	–
Articulation	*	*	–	–
Posterior fossa	*	*	×	–
Prearticular	–	*	–	*
SKULL				
Palate	*	×	–	–
Rostrum	*	–	–	×
Frontonasal hinge	*	–	*	×
Unfused prefrontals	*	–	*	*
Temporal fossae	*	×	*	*
Supraoccipital area	×	*	×	–
Quadrate articulation area	×	×	*	*

* very similar; × some similarity; – little or no similarity

IV. DISCUSSION AND CONCLUSIONS

From the above data comparing *Prophaethon* with Recent birds there would appear to be several possible hypotheses concerning its relationship to known taxa.

The species might be regarded as a charadriiform bird, showing the alcid type of pelvis and with a head adapted for catching prey in water and showing modifications which have parallels elsewhere in the taxon. But the specialized sternum with its facet for furcular attachment is not present in known Charadriiformes, and it would be necessary to argue that, since it is known in aquatic birds of two other orders, it might be an adaptation that potentially could have evolved under any similar behavioural or environmental selection pressures.

Prophaethon might be regarded as a procellariiform bird, in which case there is a precedent for a modified sternum, but the skull and rostral characters would not be typical of the known forms of that order.

If it is argued that the possession of both the specialized frontonasal hinge and the sternum are indications of pelecaniform affinities, then another assumption must be made, that a saltatory form of evolution has produced the more extremely evolved characters now present in this evolutionary diverse order while retaining more generalized characters in other structures which could presumably undergo subsequent modification. This is at variance with the apparent evidence provided by a proto-frigatebird from the Lower Eocene, described by Olsen (1974), which shows modifications in various skeletal elements of the postcranial skeleton but has not achieved either the specialized skull or the sternum typical of the Fregatidae.

If any of the above suggestions are adopted then, at least in so far as the early Tertiary is involved, the range of osteological characters used to define any of the three orders must be extended to include a number of significant characters which are at present regarded as diagnostic of some other order. The limiting groups of characters which may be used to assign any species to a particular order will then no longer be clearly separable ; we shall have to assume it is not possible to identify a bird from this geological period unless certain critical skeletal elements are available.

Alternatively, in view of the lack of evidence of affinity with any single order, it could be suggested that in the early Tertiary these three Recent orders had not yet diverged, and that *Prophaethon* was referable to an ancestral stem from which more than one Recent order had subsequently evolved. There is, however, a considerable amount of fossil bird material from this period, most of which appears to be referable to Recent families, suggesting that the degree of evolutionary divergence apparent in Recent families had already occurred by this period. In addition fossils referred to Pelecaniformes and Charadriiformes are known from the Upper Cretaceous and from the evidence available it seems that in general the ordinal divisions of birds had occurred within the Cretaceous.

Some other Lower Eocene species show this intermediacy of affinities. Among the more specialized forms described from this period is a sea-bird with bony, tooth-like projections on the jaws, *Odontopteryx toliapica* of the family Odontopterygidae. Related forms, usually separated in the family Pseudodontornithidae, are known from the Miocene. In recent studies of the British Lower Eocene we have found evidence of more numerous and varied forms of both families at this period. These birds were at first regarded as pelecaniform, but Howard (1957), in describing *Osteodontornis orri* of the Californian Miocene, pointed out that the skeleton showed a mixture of pelecaniform and procellariiform characters. The British specimens, recently prepared, appear to confirm the rather specialized nature of this group.

Avian phylogeny in the Cretaceous is still a mystery and in view of the lack of evidence speculation is of very limited use. If the Lower Eocene is taken as a base line there is an array of families known from fossil remains, most of them first known to occur at this period and subsequently persisting until Recent times. If we insert into this array both *Prophaethon* and the bony-toothed birds we may produce the kind of picture shown in simplified and linear form in Fig. 7.

Let us assume that the base line is the Lower Eocene and the lines rise to the Holocene, that A1–A3 represents charadriiform families, B1–B3 pelecaniform families and C1–C3 procellariiform families. If we insert *Prophaethon* as AB, the Odontopterygidae as BC1 and the Pseudodontornithidae as BC2, then we have a continuous sequence in which each family shares some characters with the adjacent ones and the whole presents a relatively uniform array which might have arisen as a complex adaptive radiation from a single ancestral origin, rather than as a divergence from three separate stems, yet showing some morphological convergence. If during later periods *Prophaethon* and the bony-toothed birds became extinct, then the remaining families would appear to fall into more discrete groups which are then identified as Recent orders – ordinal definition being aided by the absence of the intervening forms. The diagram presented is a linear one, but the relationships should be visualized as three-dimensional, the three Recent orders forming a triangle.

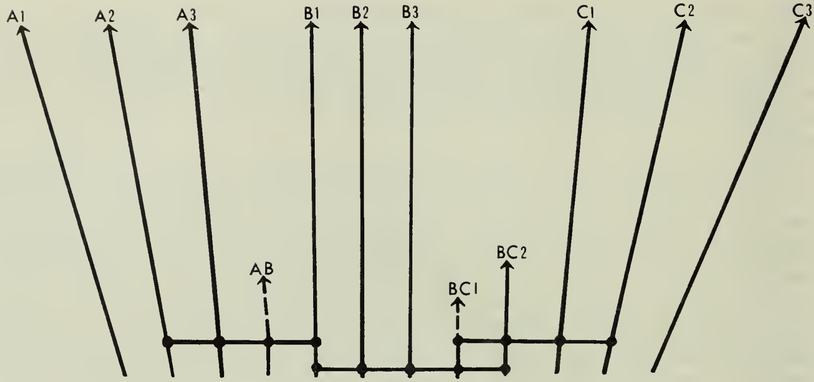

FIG. 7. Hypothetical relationship of families.

The bony-toothed birds would occupy the space intervening between the Pelecaniformes and the Procellariiformes, while *Prophaethon* would come in a more central position in view of its similarities to all three orders.

We have also indicated by transverse lines two possible distributions of shared characters resulting from the loss of some of these families. If BC1–2 disappear then the two linking characters which they share become discrete ordinal peculiarities. The character which AB is shown as sharing with families on either side would, following the extinction of AB, still persist in more than one Recent order but might be limited to certain families. If we assume A1–3 to be charadriiform families and B1 to be the Phaethontidae, species of the latter are seen to share a number of minor morphological characters with the former group and not with other pelecaniform families. The existence of such characters led to some early suggestions that the Phaethontidae had more affinity with the Charadriiformes than with the Pelecaniformes, and Mathews & Iredale (1921) created for it a suborder within their gull order, Lari. These similarities have also been explained as convergence with the terns (Sterninae of the Laridae) brought about by similar methods of feeding. The latter might be a valid explanation, but on the basis of the hypothesis proposed some at least of these similarities might be explained by a closer degree of affinity between the families involved at an earlier period and by the persistence of some shared characters.

This proposed arrangement would appear the most satisfactory to explain the combinations of characters found in *Prophaethon* and the bony-toothed birds, and to present a balanced view of sea-bird evolution in the Lower Eocene based on present evidence. There has for long been general acceptance that the pelecaniform and procellariiform birds shared a common ancestry more recent than that of avian orders in general. The suggested association of the Charadriiformes with these has been weaker and based mainly on the peculiarities shown by the Phaethontidae.

The evidence from the skeletal structure of *Prophaethon* might now justify, provisionally, a stronger linking of the Charadriiformes with the Pelecaniformes. These three Recent orders, with the two interordinal linking taxa, appear to form a more unified group, perhaps a single superorder which, for the purposes of arranging avian taxa of the Lower Eocene and earlier periods, might provide a more convenient unit than the existing groups.

This idea does not significantly conflict with present views on affinities based on the study of Recent taxa. These are summarized by Sibley & Ahlquist (1972) in their study of non-passerine relationships based on egg-white protein electrophoresis. There are various characters which appear to link the three Recent orders, and in addition the Gaviiformes are considered to be closely related to the Charadriiformes and the Sphenisciformes to the Procellariiformes. These two additional orders should perhaps be included in any proposed major grouping. Sibley & Ahlquist found evidence of similar starch gel egg-white patterns in Sphenisciformes, Gaviiformes, Procellariiformes, Charadriiformes, and possibly the Pelecanidae, Fregatidae and Phaethontidae. There is therefore evidence of a large and interrelated supra-ordinal group, within which some earlier links may still be undiscovered.

While this hypothesis may help to establish the position of *Prophaethon* within the framework of palaeontological phylogeny, the problem of fitting it into the existing taxonomic hierarchy still remains. As we have already indicated, it does not show definite affinity with any single existing taxon and to attempt to associate it with one of these would affect ordinal definitions based on osteology. From a nomenclatural point of view the alternative treatment of the specimen seems preferable whereby its isolated position is recognized. In terms of Recent taxonomy *Prophaethon* constitutes an interordinal link. For nomenclatural purposes it seems preferable to treat it as a monotypic order, Prophaethontiformes, with the single family Prophaethontidae, while recognizing its special character. It is then possible to insert it into the existing framework without unduly affecting existing taxa, and it can be merged with another taxon at a later date if new and overriding evidence should justify this. For the moment we would recommend that its placement should be between the Pelecaniformes and the Charadriiformes.

V. SYSTEMATIC DESCRIPTION

Order PROPHAETHONTIFORMES nov.

ORDINAL DIAGNOSIS. Dorsal surface of skull with prominent postorbital process and deep, rounded temporal fossae. Cranium small. Anterior lateral surface of frontal flattened for attachment of unfused prefrontal. Deep fronto-nasal hinge with prominent brow ridge. Lateral nasal struts lie alongside, and may fuse with, rostrum just anterior to hinge. Elongated, oval depression in roof of orbit bordering external edge. Zygoma laterally flattened with no dorso-ventral torsion at anterior end. Rostrum tapering evenly with nares approaching schizorhinal condition but terminating anterior to fronto-nasal hinge. Elongated nasal aperture extending almost to rostral tip. Palate typically schizognathous. Quadrate with large projecting flange on otic process, and posterior lower end of shaft with deep, narrow groove. Lower mandible long and slender. Dentary with horizontal external groove. Posterior mandibular fossa large, not perforating external wall. Prearticular large.

Carina of sternum deep, with curved ventral edge and anteriorly projecting apex with well-developed manubrial spine. Flattened anterior surface at carinal apex for articulation of furcula, and carinal tip bifurcated. Coracoid sulcus shallow with poorly-developed ventral lip. Ventral labial prominence projecting and rounded.

Coracoid with large sterno-coracoid surface, slightly curved ventrally, and sternal facet wide. Small facet for labial prominence on ventral surface. Procoracoid stout, projecting laterally and curving anteriorly. Coracoid fenestra present. Glenoid facet projecting dorso-ventrally.

Pelvis elongated and relatively narrow, with prominent median dorsal ridge, and narrow posterior shield between raised posterior iliac crests. Fused synsacrum with greatest depth at anterior end, tapering posteriorly. Last thoracic vertebra not fused to synsacrum. Anterior iliac plates sloping down steeply and curving outwards to form broad, lateral flanges which project a little anterior to end of the synsacrum.

Femur with internal cotylar surface internally deflected towards distal end. Proximal trochanter has abrupt obturator ridge with hollow on posterior side. Trochanteric ridge prominent.

Inner cnemial crest of tibiotarsus extending proximally well beyond anterior surfaces, as a thin flange projecting prominently, with some external curvature at outer edge. Outer cnemial crest thicker distally than inner crest, with proximal end terminating at an angle a little proximal to articulating surfaces. Internal articular surface with a posteriorly projecting curved lip.

Family **PROPHAETHONTIDAE** nov.

DIAGNOSIS. The only family of its order.

Genus ***PROPHAETHON*** Andrews 1899

DIAGNOSIS. The only genus of its family.

TYPE SPECIES. *Prophaethon shrubsolei* Andrews.

Prophaethon shrubsolei Andrews 1899

(Pls 1–3 ; Figs 1–6)

1899 *Prophaethon shrubsolei* Andrews : 776–785, pl. 51.

DIAGNOSIS. The only species of its genus.

HOLOTYPE. Imperfect skull, lower jaws and hyoids, sternum, right coracoid, distal end of left coracoid, left scapula, right femur, proximal end of left tibiotarsus, 11 vertebrae, rib fragments and synsacrum. In British Museum (Natural History), Department of Palaeontology registered number A683.

LOCALITY AND HORIZON. Lower Eocene, London Clay (Ypresian) of Sheppey, Kent, England.

VI. ACKNOWLEDGMENTS

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VIII. INDEX

The page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.